Perspectives

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Revision of Fisher's Analysis of Mendel's Garden Pea Experiments

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R. A. Fisher (1936) made the assertion that the data in Mendel's experiments with garden peas (Mendel 1866) were too close to expectation. One of the most striking examples seemed to be the six experiments with plant characters designed to test the theoretical 2:1 ratio of heterozygotes (*Aa*) to homozygotes (*AA*) among F_2 plants exhibiting the dominant trait. In each of these experiments, 100 F_2 plants showing only the dominant trait were selfed, and 10 seeds from each were planted. When a mixture of dominant and recessive traits was observed among the 10 resulting plants, Mendel classified the F_2 as heterozygous, and when the 10 plants all had dominant traits, Mendel classified the F_2 as homozygous. Mendel observed a 1.99:1 ratio overall in these data, and he concluded that the six experiments agreed with a 2:1 ratio. Fisher pointed out that occasionally (5.6% of the time) a heterozygous F_2 would have 10 dominant-trait offspring in a row by chance and that therefore the expected experimental ratio by Mendel's methods should be 1.7:1, and not 2:1. Thus, Fisher concluded that some sort of bias must have entered into the execution of these experiments or the presentation of the data.

This key conclusion of Fisher has been challenged by E. Novitski (2004, accompanying article in this issue). First, it is highly unlikely that Mendel could plant 6000 plants (six experiments × 100 F_2 plants × 10 seeds planted) with no losses. Novitski points out that Mendel does not give the rate of failure data for his 2:1 ratio experiments, but in a subsequent experiment of Mendel's, he mentions a 2% (11 of 556) failure of seeds to germinate and survive. Then, if some sets of 10 were observed to have 9 or fewer surviving plants, what would Mendel have done? It would be perfectly clear to Mendel that a set of 9 or fewer plants that had a mixture of dominant and recessive traits must have come from a selfed heterozygote, and Novitski persuasively argues that Mendel would have counted those, correctly, as heterozygotes. Second, in those cases in which there were 9 or fewer plants, all with dominant traits, Mendel would not have the 10 he specified as the number he "cultivated," and because he would be less certain that the selfed F_2 were indeed homozygous, it is highly plausible that Mendel would have redone those sets of 10 (or used extra sets of 10 planted in anticipation of inevitable losses).

The result of Novitski's proposal is that there are two effects on the expected ratio: the undercounting of heterozygotes in sets of 10 dominant-trait plants and the undercounting of homozygotes when sets of 9 or fewer dominant-trait plants are discarded. The expected quotient, *R*, of those counted as heterozygotes divided by those counted as homozygotes is calculated as follows. Those counted as heterozygotes are the sum of the following products: the fraction of F_2 plants that are actually heterozygous (two-thirds), the probability of sets of a certain number of surviving plants (based on a failure rate, q), and the probability that that certain number of plants includes at least one with the recessive trait. Those counted as homozygotes are the product of the probability that all 10 plants will survive, and the sum of the fraction of the F_2 plants that are actually homozygous plus the fraction of F_2 plants that are actually heterozygous times the probability of a heterozygous F_2 plant giving rise to all 10 dominant-trait offspring. This simplifies to the formula for *R*, the ratio of those counted as heterozygotes (*Aa*) to those counted as homozygotes (*AA*),

$$R = \frac{\sum_{i=1}^{10} P(i)\{1 - (3/4)^i\}}{P(10)\{(1/2) + (3/4)^{10}\}},$$

where $P(i)$ is the binomial distribution,

$$P(i) = \frac{k!}{i!(k-i)!} p^i q^{(k-i)},$$

$k = 10$ seeds sown, $i =$ the number of successful seeds

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out of 10, and $q = 1 - p =$ Mendel's germination and survival failure rate. R is not dependent on the number of sets counted. R is the same in the replacement sets as it is in the initial sets counted, so when the counts are combined, the equation stays the same. Substitution of the best estimate of Mendel's germination and survival failure rate of 2.0% yields an expected experimental ratio of those counted as heterozygotes to those counted as homozygotes of 2.068:1. This indicates that not only are the two effects opposite each other, but also, because they are of a similar order of magnitude, they almost cancel each other out. This ratio of 2.068:1 is not statistically significantly different from the ratio observed by Mendel in the six experiments with plant characters with 100 F_2 plants analyzed in each experiment (violet:white flower color, 64:36; tall:dwarf, 72:28; full:constricted pods, 71:29; green:yellow pods, 60:40; axial:terminal flowers, 67:33; green:yellow pods repeated, 65:35; in each case $\chi^2 < 2.6$, $P > 0.1$). This ratio of 2.068:1 is consistent with the ratio of ~2:1 estimated by Novitski (2004, accompanying article).

A good estimate of Mendel's germination and survival failure rate is the 2.0% (11 of 556) based on Mendel's data in a subsequent experiment. A second approach to estimating the survival rate is to find the q value in the equation for R such that the sum of the chi-square values for all six experiments is minimized. This leads to an alternative estimate of Mendel's failure rate, q, of 1.54%. Substituting that latter value of q into the equation for R gives a numerical value of the expected ratio in Mendel's experiment of 1.975:1, which also is not statistically inconsistent with the data of Mendel's six experiments.

In summary, the significance of R. A. Fisher's criticisms (Fisher 1936) of Gregor Mendel's data (Mendel 1866) being too close to expectation has been explored by numerous authors, two different approaches to which are reflected in Edwards (1986) and Novitski (1995). Fisher's points regarding the six experiments testing the 2:1 ratio are perhaps of greatest concern, inasmuch as Mendel is not too close to the right expectations, which Fisher asserts should be 1.7:1, but rather close to what Fisher viewed as the wrong expectations. Novitski (2004, accompanying article) has challenged Fisher's conclusion in the case of these six experiments by taking into account the low likelihood of losing none of the 6000 plants and by pointing out persuasively how Mendel would undoubtedly have correctly classified as heterozygotes those F_2 plants yielding sets of 9 or fewer offspring of dominant and recessive traits, while those sets all dominant, but fewer than 10, may well have been discarded owing to greater uncertainty as to their genotype. The exact calculation for the expected ratio of those classified as heterozygotes to those classified as homozygotes, based on the rate of failure q, is provided by the equation for R. For q equal to Mendel's 2% failure rate, the ratio is 2.068:1. This ratio is not statistically different from the ratios seen in Mendel's data and is much closer to the ratio that Mendel observed than to the ratio that Fisher proposed. Thus, while it can still be said that many of Mendel's results are surprisingly close to the theoretical expectation, Novitski (2004, accompanying article) has made the plausible argument that Mendel may well have stood inappropriately criticized for not having data close to Fisher's ratio of 1.7:1 in the case of these six experiments.

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